The effects of grey seal predation and commercial fishing on the recovery of a depleted cod stock

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Cod (*Gadus morhua*) are preyed upon by grey seals (*Halichoerus grypus*) and there is debate over the impact this has had on the decline of stocks and their prospects for recovery. We analysed a depleted stock to the West of Scotland and show that seal predation rate is consistent with a type II functional response. Forward projections of a model including the functional response under varying levels of fishing and seal population size suggest that stock recovery is possible under current conditions but there is a modest probability that the stock will decline further in both the short and long term. The potential recovery is fragile and sensitive to relatively small increases in either fishing or seal predation. Forward projection models that exclude the functional response estimate a lower probability of stock decline and may underestimate the risk to the stock. At low stock sizes and high fishing mortality rates functional response models project slower recovery but the opposite is true at low fishing mortality.
1. Introduction

Fisheries for Atlantic cod (*Gadus morhua*) have long existed and provide an important source of food as well as supporting valuable commercial trade (Kurlansky, 1997). Many cod stocks both in Europe and North America have declined to low levels (Cook et al., 1997; Myers et al. 1996) and the species is currently classified as “vulnerable” in the IUCN Red List (IUCN, 2014). Grey seals (*Halichoerus grypus*), classified as “least concern” by the IUCN (IUCN 2014), are predators on cod (Prime & Hammond 1990; Hammond, Hall & Prime 1994; Hammond & Grellier 2006) and potentially compete with fisheries for the same resource. As a result there is controversy over the impact of seal predation on fisheries (Harwood 1984). Recent estimates of the mortality due to seal predation have suggested that it may be of sufficient magnitude to impair stock recovery both in Europe (Cook et al. 2015) and Canada (Fu, Mohn & Fanning 2001; Trzcinski, Mohn & Bowen 2006; O’Boyle & Sinclair 2012; Swain & Mohn, 2013; Swain & Benoit, 2015). By contrast, a report to the European Parliament Committee on Fisheries concluded that the effect of seal predation on fish stocks in Scottish waters was insignificant (Boyd & Hammond 2010).

An impediment to the evaluation of the effects of seals on fish populations is that the estimation of predation rates presents considerable challenges because data on diet and quantities of fish eaten by seals are hard to acquire. Thus the study by Boyd and Hammond (2010) relied on estimates of fishing mortality rates and stock biomass that were made on the basis of fixed natural mortality rates which did not account for seal predation explicitly, making comparisons between fishing and separately estimated seal predation debatable. Similarly, performing stock assessments without accounting for seal predation (where it may be large) can lead to biased estimates of fishing mortality that give a misleading impression of the ability of managers to influence stock biomass by controlling exploitation in the fishery. In order to avoid this problem it is necessary to estimate stock biomass, fishing mortality and seal predation as part of the same stock assessment so that the respective estimates are calculated on the same basis and are internally consistent.
Typically in the ICES area fish stock assessments only account for non-fishing mortality as a constant estimated externally to the assessment itself. This may include estimates of seal predation, as in some North Sea assessments, where natural mortality values used are derived from multispecies models that account for such predation (ICES 2014a). Nevertheless these are treated as fixed values in single species assessments and the resultant estimates of fishing mortality are not necessarily consistent with those derived from the multispecies analysis. In this paper we estimate seal predation and fishing mortality to show the importance of accounting for both these mortalities in a single assessment. We infer a relationship between the seal predation rate and stock biomass, and between stock biomass and subsequent cod recruitment. This allows a full population dynamics model to be constructed which we use to investigate stock trajectories under different scenarios of seal population size, seal predation rate and fishing mortality.

The West of Scotland cod is taken as an example of where such an approach is feasible because samples exist of seal diet and cod consumed. Recent assessments by the International Council for the Exploration of the Sea (ICES) show a major decline in spawning stock biomass (ICES 2014b) with high and relatively constant fishing mortality since the 1980s. The decline in biomass reflects similar trends in adjacent cod stocks in the Irish Sea and North Sea. Management advice is effectively to avoid all catches of cod (ICES 2014b). The stock is subject to a “recovery plan” that is intended to reduce fishing mortality and increase the biomass through fishing effort limitation, gear modifications, and landings limits (Kraak et al. 2013). The assessments assume fishing mortality is the principal cause of stock decline, with the implication that reducing fishing mortality will favour stock recovery. Cod may account for approximately 10% of the seal diet on the West of Scotland with an estimated consumption amounting to three times the official landings in 2002 (Harris 2007), yet ICES assessments do not explicitly consider this mortality. This would suggest that a recovery plan based on assessments which exclude seal predation may be unreliable. The analysis presented here considers how seal predation affects the perception of stock recovery scenarios.
2. Methods

Cook et al’s (2015) assessment model is used as the basis of the analysis but is extended to include the period after 2005 and considers the full dynamics of the cod population and the relationship between prey population biomass and seal predation.

Our approach involved estimating historical values of the cod stock biomass and mortality rates and then projecting these forward under different assumptions about seal population size and fishing. The projections were done using a stochastic model that takes account of uncertainty in the model parameters and the structural relationship between stock size and recruitment (annual number of cod at age 1).

We used standard fishery data reported in ICES (2014b) that comprise fishery catch at age and relative abundance estimates from research vessel surveys, and cover the period 1985-2013 as listed in Table 1. Although there are fisheries data prior to 1985 there are no seal diet data during this earlier period making estimates of seal predation problematic so we restricted the analysis to the more recent period when diet data are available. In order to estimate seal predation rates we used data on cod length compositions in the seal diet, and total cod biomass eaten reported by Harris (2007). Seal population numbers estimated by the UK Sea Mammal Research Unit (SMRU) (SCOS 2014) for the Hebrides were used as the population exploiting fish in the West of Scotland as it is predominantly these animals that forage in the area (Harris 2007). Over the time period considered the grey seal population in the area has increased from about 27,000 to 30,000 though in recent years it has remained stable. In contrast seal populations foraging in the North Sea have increased.

Data on cod consumption by seals was only available for 1985 and 2002. The data were analysed using an age structured stock assessment model outlined below, which is fully documented in Cook et al (2015). The population of cod $N$ at age $a$ in year $y$ decays exponentially as a result of a total mortality, $Z$;
The total mortality is partitioned between fishing mortality $F$, natural mortality $M$ and seal predation mortality $P$ as:

$$Z_{a,y} = F_{a,y} + M_{a,y} + P_{a,y}$$

Fishing mortality is assumed to be the product of an age effect or selectivity, $s$, and a year effect (fishing effort), $f$:

$$F_{a,y} = s_{a,y} f_y$$

Where the age and effort component follow an autoregressive process with variances $\sigma_f^2$ and $\sigma_s^2$:

$$f_y = f_{y-1} \exp(\varepsilon_{f,y}), \quad \varepsilon_{f,y} \sim \text{Normal}(0, \sigma_f^2), \quad y \neq 1$$

$$s_{a,y} = s_{a,y-1} \exp(\varepsilon_{s,a,y}), \quad \varepsilon_{s,a,y} \sim \text{Normal}(0, \sigma_s^2), \quad y \neq 1$$

Natural mortality $M$ is assumed to be dependent on size and given by the Lorenzen (1996) equation:

$$M_{a,y} = A \bar{w}_{a,y}^B$$

Where $\bar{w}$ is the mean weight at age and $A$ and $B$ are constants.

Seal predation mortality is modelled as the product of a size preference (or selectivity), $s_{\text{seal}}$, and an "effort" component, $q G$, where $q$ represents the annual per capita capacity of seals to prey on cod (the "predation rate"), and $G$ is the abundance of seals. The seal predation mortality is thus:

$$P_{a,y} = s_{\text{seal},a,y} q_y G_y$$

The quantity $q$ will depend on the ability of seals to find and catch cod, the time it takes to process prey items and the presence of other prey and may change over time. To avoid any structural assumptions between predation rate and prey abundance $q$ is assumed to follow a simple autoregressive process with variance $\sigma_q^2$:

$$q_y = q_{y-1} \exp(\varepsilon_q), \quad \varepsilon_q \sim \text{Normal}(0, \sigma_q^2)$$
Assuming seals prefer a size range of cod, their selectivity is modelled as function of mean fish length at age, $\tilde{L}$, using gamma shaped curve with constant parameters $\alpha$ and $\beta$ (Millar & Fryer 1999):

$$s_{\text{seal},a,y} = \left(\frac{\tilde{L}_{a,y}}{\left[(\alpha-1)6\right]}\right)^{\alpha-1} \exp(\alpha-1-\tilde{L}_{a,y}/6)$$

We also calculated the “partial biomass” (PB) of cod available to seals as the sum of the biomass at age in the stock weighted by the size selectivity of the seals:

$$PB_y = \sum_a s_{\text{seal},a,y} w_{a,y} N_{a,y}$$

We fitted the model using the Bayesian statistical package WinBUGS (Lunn et al. 2000) configured as described in Cook et al 2015 but with minor changes to include more recent catch data. Observed landings, discards, survey indices and total consumption of cod by seals were assumed to be lognormally distributed. The numbers of cod at length in the seal diet were assumed to be multinomially distributed. In the original assessment model catch data were split between observed cod landings and discards, with each data component fitted separately in the model with different observation errors. The model assumes fixed discard size selection over time. Catch data beyond 2005, however, comprise almost entirely discards with a different pattern of discarding. Hence, in order to extend the model to 2013 we treated the catch data from 2006 onwards as an aggregate of landings and discards and fitted the model to the total catch at age with a new observation error distribution. This circumvents the need to estimate discard selection for this period. In all other respects the model was the same as the original. We saved a random subset of 1000 samples from the Markov Chain Monte Carlo (MCMC) simulation for all model parameters for subsequent use in the projection model described below.
Since the ICES cod assessment is the recognised standard for fishery advice we compared our stock biomass and fishing mortality estimates to their most recent assessment (ICES 2014c) as a check of consistency. Since this assessment only gives a time series back to 1981 we also compared the estimates to the 2002 assessment (ICES 2002) as this provides stock estimates back to 1966, giving a longer perspective on changes to the biomass. Each of these assessments uses different values for natural mortality, $M$, which has the effect of rescaling the biomass estimates. Higher values of $M$ give larger values of biomass. In order to compare trends across assessments we rescaled the biomass from the two ICES assessments to give the same mean biomass for the period 1985-2002 as our assessment. This is the period when all three series overlap.

We used equations 1-6 and 8 as the basis for a stochastic forward projection model. The input quantities used are listed in Table 2. Each realisation of the model was based on one of the MCMC samples. For each random draw we fitted Ricker (1954) and Beverton-Holt (1957) stock recruitment models by least squares to the sample time series of stock-recruitment pairs assuming lognormal errors. We estimated both parameters in each model and chose the model with the lowest AIC to forecast recruitment. Annual recruitment variability was then simulated by bootstrapping residuals from the fitted model.

It is possible that annual recruitment residuals are correlated as the result, for example, of an environmental trend. We examined the residuals after fitting the Beverton-Holt model to the mean stock and recruitment values from the stock assessment model but found no evidence of a time trend (Figure S1.1, supplementary material) so treated the bootstrapped residuals in the simulation model as independent.

In the case of seal predation we fitted a type II functional response (Holling 1959) to model the relationship between seal predation rate ($q$) and cod partial biomass of the form:

$$ q_i = c/(1 + cdP_{Bi}) $$
where $c$ and $d$ are constants. This relationship assumes that the biomass of other prey remains constant.

Annual variability in $q_y$ was simulated by bootstrapping the residuals from the model fit. We examined the residuals after fitting the model to the mean partial biomass and $q_y$ values from the stock assessment model but found no evidence of a dependence on biomass (Figure S1.2, supplementary material) so treated the bootstrapped residuals in the simulation model as independent.

The projection model differs from the stock assessment model in using structural functions to describe stock-recruitment and $q$-partial biomass relationships. While it is possible to fit these relationships within the assessment model doing so imposes a particular structural form on the model estimates, and in the case of the functional response in particular, there are very few data to adequately inform a parametric relationship. Estimating the recruitment values and $q_y$ values in the assessment model without an assumed functional form allows the exploration of a variety of structural relationships to be investigated in the projection phase.

To test that the projection model using a type II response was consistent with the stock assessment trend we ran the projection model from a base population biomass estimated for 1985 forward to 2013 and compared the median projected population to the population trajectory derived from the stock assessment model assuming the same historical time series of fishing mortality and seal population size.

To investigate the conditions for recovery of the cod stock we projected the population forward for 50 years from the base year of 2013 under a range of combinations of fishing mortality and seal population size. For fishing mortality we scaled the 2013 population estimate by values ranging from 0.6 to 1.8, in increments of 0.1. This range corresponds to a larger interval compared to the observed range (0.74-1.64) from the stock assessment. In the case of the seal population we scaled
the estimated 2013 population by values ranging from 0.8 to 1.2, in increments of 0.1. This narrower range reflects an assumption that the seal population is unlikely to change substantially without human intervention.

Since cod stock recovery is considered urgent we considered the probability of the cod spawning stock biomass increasing above the 2013 level by the fifth year of projection. We also assumed that by year 50 the population would be in equilibrium and calculated the median cod spawning biomass under the various scenarios.

For comparison to a fixed natural mortality rate projection we ran the model assuming that the seal predation rate was independent of cod biomass by setting \( c = \text{mean}(q_y) \) and \( d = 0 \) in equation 10 and set the seal population multiplier at 1. This scenario therefore is equivalent to status quo seal numbers and will result in non-fishing mortalities that have a stationary mean over time and most closely resembles current practice when making forward projections for this stock.

In order to test the sensitivity of the projections to the assumption of a type II functional response we also ran the model at constant seal population under two additional models for seal predation rate. Firstly, \( q_y \) values were simply projected forward using the time series model (equation 7) from the base value estimate in 2013. This allows the seal predation rate to vary independently of prey biomass. Secondly, we fitted a loess function to capture the relationship between \( q_y \) and partial biomass rather than the parametric relationship in equation 10. This allows the MCMC samples to determine the shape the functional response relationship and potentially could allow a type III response to occur.

3. Results

The estimated trend in cod spawning stock biomass from the ICES assessments and the current analysis suggests that the biomass has declined from a value close to 80000 tonnes in the mid-1960s to around 11000 tonnes in recent years (Figure 1a). There is close agreement in the trend between
the assessments although the current analysis indicates higher values in recent years compared to
the ICES assessment. The two ICES assessments show comparable trends in fishing mortality (Figure
1b) though the 2002 assessment shows a sharp decline at the end of the time series. Our analysis
shows a lower fishing mortality which declines over most of the period but an increasing trend in
recent years. This difference is due to the fact that our model allocates an increasing proportion of
the total mortality to seal predation rather than fishing. Both the ICES assessments and our
assessment give similar estimates of total mortality and is the reason why the biomass estimates are
alike (Cook et al. 2015). Full details showing the model fit to the observations are given in
supplementary material (Figures S2.1 to S2.10).

Figure 2a shows the relationship between cod spawning stock biomass and recruitment at age 1. The
fitted model, based on the mean values from the stock assessment, is a Beverton-Holt relationship
which was selected most frequently in the stochastic projections. Figure 2b shows the seal predation
rate as a function of cod partial biomass. The predation rate, q, declines with increasing cod biomass
and, in effect, results in a type II functional response. The fitted line (solid) is equivalent to the disc
equation (Holling 1959). Also shown is the loess smoothed relationship (dashed line) which suggests
that q, may decline at the lowest partial biomass and captures some elements of a type III response.

By applying the relationship in Figure 2b it is possible to calculate total mortality, Z, for combinations
of partial biomass and fishing mortality. The resulting contour plot is shown in Figure 3 for the type II
response (equation 10). Over-plotted in the figure are the observed values from the stock
assessment. It can be seen that as the cod partial biomass and fishing mortality have declined over
time the total mortality has changed little and followed the contour Z=1.2 throughout the recent
history of the stock. It shows that despite reductions in fishing mortality, the simultaneous decline in
biomass has meant that seal predation mortality has compensated for this reduction.

The functional relationships shown in Figure 2 provide the basis of the forward projection model by
forecasting recruitment and reflecting changes in seal predation rate as the biomass develops. The
projection model using equation 10 for the functional response is compared to the historical estimates of biomass in Figure 4. The median projected biomass follows the observed values for the first 13 years but thereafter tends to increase while the observed values decline and level off.

Although the projected values lie below the median, they remain within the 95% credible interval in the region of the 15th percentile. Other functional response models produced qualitatively similar results and are not plotted.

The results of the short term projection which considers the probability of the spawning stock biomass in year 5 falling below the 2013 base value are shown in Figure 5a. At current rates of fishing and seal numbers the probability of further decline is around 0.17. At equilibrium, the probability that the stock is below the base value is higher at about 0.25 (Figure 5b).

Figure 6 shows the median cod spawning stock biomass at equilibrium under different combinations of seal populations and fishing mortality. At the current rate of fishing and with the existing seal population, the median equilibrium spawning stock biomass would be close to 40000 tonnes. This represents an increase over the current biomass but is about half the biomass estimated in the mid-1960s. To achieve the latter would require a reduction in fishing mortality of about 20% or a very much larger reduction in the seal population.

The projections under stationary seal population size are summarised in Figure 7. For a constant seal predation rate the perceived risk of stock decline is lower under this assumption than a type II response both in the short and long term. The projected median biomass is almost identical to the full model for the five year projection but in the long term there are major differences. At low fishing mortality the stationary natural mortality scenario gives lower biomass values while the converse is true for high fishing mortalities. This shows that for a heavily exploited stock, if there is a predator type II functional response, there is a danger of underestimating the risks of stock decline and overestimating future biomass.
The sensitivity of the projected biomass to the functional response assumption can be seen in figure 2 which shows probability of decline and spawning stock biomass for the time series model of $q_y$ and the loess smoothed $q_y$-partial biomass relationship. For the five year projection the loess model gives the highest probability of stock decline at intermediate fishing mortality rates. The same model gives almost identical results to the type II response for probability of decline at year 50. The time series model gives a much higher long term risk to the biomass because it assumes the 2013 value (which is high) is propagated forward regardless of stock size. In general, the effects of the different assumptions on seal predation rate are largest at equilibrium due to the cumulative effects of predation, fishing and recruitment. The type II and loess models shows the greatest change in equilibrium spawning stock biomass as a function of fishing mortality as they assume a dynamic relationship between predation rate and prey biomass. The same models also suggest higher probability of stock decline in the short term than the fixed natural mortality model.

4. Discussion

Both the ICES and the current analysis, which includes seal predation, estimate a long term reduction in the cod spawning stock biomass. In recent years the decline has halted with perhaps a slight increase. Unlike the ICES assessment our analysis suggests the fall in biomass has occurred in the presence of diminishing fishing mortality but almost constant total mortality (Figure 3) indicating that other mortalities have compensated for reduced fishing. The compensation appears to be a result of the effect illustrated in Figure 2b that the seal predation rate increases as partial cod biomass decreases and is typical of a type II functional response. Such a response has been reported before for grey seals (Middlemas et al. 2006). Smout et al (2013) also estimated functional responses for seals but found evidence of prey switching based on data at a much finer spatial scale. Our analysis offers little evidence of prey avoidance at low biomass values as implied by predator switching, perhaps because the spatial resolution in the assessment data is absent.
We were able to incorporate the seal functional response and the stock recruitment relationship into a cod stock projection model that generated biomass trajectories consistent with historically estimated values (Figure 4) and hence supported use of the model to project the stock beyond the current level. The 5 year ahead and long term projections indicate that there remains a risk that the biomass will not increase at current rates of fishing and seal population (Figure 5). However, the biomass is close to the lowest observed and this risk is large compared to the conventional probability of 0.05 used by ICES to determine rates of fishing that ensure the lowest spawning stock is avoided. There is also some indication that the projection model may, if anything, be over-optimistic since the observed cod biomass lies near the lower range of 95% CI of the projected population (Figure 4). This may be the due to model misspecification of the seal functional response or to changes in biological factors such as cod maturation rates and fecundity which would change the estimated stock-recruitment relationship. There may also be a numerical response by predators to local abundance not accounted for in the model or arising from seal herds in the North Sea foraging in the West of Scotland. The latter seems less likely as fish stocks are at higher abundance in the North Sea and seal tracking data do not show this movement (McConnell et al 1999).

The divergence between the observed stock biomass and the projected population from the simulation model in more recent years might be the result of an environmental effect on recruitment. In the adjacent North Sea area, for example, there is evidence of a negative temperature effect on cod recruitment (O’Brien et al 2000; Cook & Heath 2005). Rising temperature or a climatic trend could therefore explain weaker than expected recruitment in recent years which would contribute to a decline in the stock biomass. The recruitment residuals for the West of Scotland, however, show no time trend indicating that such an effect is difficult to detect. The relationship between stock size and recruitment appears to be able to explain much of the dynamics but will not capture environmental effects.
With status quo seal populations and current (2013) fishing mortality prevailing over the long term, median cod spawning stock biomass is projected to be higher than current levels but below the earliest observed values (Figure 6). It suggests that in the long term current fishing rates, which are close to the historical minimum, should allow some stock recovery provided the stock-recruitment relationship holds in the future. However, an increase in the seal population of only 10% could reduce the long term median biomass from 40000 tonnes to little more than 30000 tonnes. Both the equilibrium analysis and the short term projection therefore indicate that the prospects of stock recovery under current conditions are fragile. Our stock assessment suggests that fishing mortality in recent years has tended to increase and, if sustained, would further compromise stock recovery.

The SMRU estimates of the size of seal population in the West of Scotland indicate little change for a number of years (SCOS 2014) and if this continues there would be no change to the risk of recovery of the cod stock. Seal populations in Europe have a measure of protection under a variety of European and national legal instruments reflecting a public desire to conserve them. European Union regulations (EU 2009), for example, restrict the trade in seal products effectively outlawing a market in Europe and hence removing any incentive to hunt seals. In the UK, legislation places restrictions on the killing of seals and methods of slaughter while allowing the shooting of seals under certain limited conditions (HMSO 1970). Although the protection is not absolute, no systematic hunting or large scale culling of grey seals in the UK has taken place since 1978 and populations around the British Isles have increased for a number of years (SCOS 2014) though the recent increase has taken place mainly in the North Sea. As human intervention to control seal population size is unlikely it means the cod recovery can only be enhanced by reducing fishing mortality.

Our analysis implicitly assumes that the cod stock in the West of Scotland is well mixed and equally available to both seals and the fishery. This may not be the case. Studies in the Celtic Sea and North Sea suggest that seals forage in areas away from areas of high fishing activity (Matthiopoulos et al.)
There are also likely to be areas where seals are able to forage where commercial fishing is not possible. Hence the fishery and seals may exploit different cod populations and avoid competition. If correct this would mean the estimated impact of seal predation in our analysis is too high. While cod are known to exhibit site fidelity many individuals migrate between spawning and feeding grounds or show dispersal behaviour (Robichaud & Rose 2004; Neuenfeld et al. 2013). A comprehensive analysis of genetic material in the Northeast Atlantic indicates that the West of Scotland population is indistinguishable from adjacent stocks (Heath et al. 2014). This suggests the population is well mixed and while seals and the fishery may operate in different areas they are probably not exploiting discrete populations. It seems that sufficient exchange is likely to occur to justify the modelling assumptions.

An obvious weakness in the analysis is the paucity of seal consumption data to parameterise the functional response in the projection model. Only two years of data were available for analysis with the most recent observation made in 2002, more than a decade before the base year used for projections. However, the two samples come from years when the cod stock was in very different states providing considerable contrast in the data to inform the model. In both years the consumption of cod by seals was in the region of 6000 tonnes while the spawning stock biomass of cod reduced by approximately 60% over the same period. Sampling of seal diets around the British Isles occurred in 2010 and 2011 and preliminary estimates of consumption appear similar to the earlier years (Hammond, pers comm) and this is consistent with the estimated seal consumption for these years from our stock assessment model.

Bias may arise in the estimates of seal predation if the scat samples on which the diet is determined do not adequately reflect true seal food intake. The samples themselves may not be truly random since they are collected at accessible haul out sites. Furthermore, if larger fish are only partially consumed, leaving the head uneaten, the otoliths on which the seal diet it determined will be absent leading to bias toward small fish in the estimated size range consumed. If large fish are under-
represented in the samples predation on younger fish will be over-estimated (and vice-versa for older fish). It could imply a greater impact on the cod spawning stock because total mortality on larger fish would be proportionately larger than currently estimated. Clearly these are sources of potential bias and uncertainty that merit further investigation.

The Lorenzen relationship used to account for other non-fishing mortalities (equation 5) assumes that all non-fishing mortality (including seal predation) is subsumed in the estimate which means that our estimates of seal predation may be biased low. However in fitting the stock assessment model we estimated the constants of the equation which allows the relationship to adjust downward in the presence of seal consumption data. On average, our estimates of natural mortality from the fitted Lorenzen equation were 25% lower than those from calculated the nominal values in Lorenzen (1996) which indicates bias may be accounted for in the model fit.

The type II functional response assumed in the projection model implies that the predation rate by seals increases as the partial biomass of cod decreases. This means that for a fixed fishing mortality, if the biomass is in decline, the total mortality rate will increase and accelerate that decline. The converse of this effect is that total mortality will decrease if the cod biomass is increasing and will accelerate any recovery. For the West of Scotland cod, provided fishing mortality can be reduced to a level sufficient to bring about some biomass increase, seal predation should diminish and further aid stock recovery. These effects would be modified in the presence of a numerical response by seals, especially if the distribution of cod became more patchy when total abundance changes.

The principal difference between the projection model developed here and those more usually applied to evaluate future stock development is that reductions in fishing mortality rate do not necessarily translate into reduced total mortality acting on the stock. Consequently a random fluctuation producing poor recruitment, for example, could reduce stock biomass and cause an increase in seal predation that negates a reduction in fishing mortality rate. At low stock biomass
such effects can increase the risk of further stock decline and predict lower biomass compared to models which assume seal predation rate is constant.

The debate about the cod-seal interactions can be polarised with protagonists suggesting that the decline (or lack of recovery) in cod populations is either the result of fishing or that seal predation is responsible. If the “fishing” hypothesis is correct then the obvious solution is to reduce fishing, while if the “seals” hypothesis is true then cod recovery can only occur if predation can be reduced, essentially through a seal cull. From the perspective of the cod, death as a result of fishing or predation is equally unattractive. Its problem is that the total mortality, from whatever source, is high enough to either cause population decline or prevent recovery. Reducing that total mortality can be influenced by human intervention but how that intervention occurs will depend on the relative value of seals, cod and the fishery to society.

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References


Cronin, M. A. Gerritsen, H & D. Reid. 2012. Evidence of low spatial overlap between grey seals and a specific fishery off the west coast of Ireland. Biological Conservation 150, 136-142.


Neuenfeldt, S., Righton, D., Neat, F., Wright, P. J., Svedäng, H., Michalsen, K., Subbey, S.,
Steingrund, P., Thorsteinsson, V., Pampoulie, C., Andersen, K. H., Pedersen, M. W. and Metcalfe,
J. 2013. Analysing migrations of Atlantic cod Gadus morhua in the north-east Atlantic Ocean:
Prime, J.H and Hammond, P.S. 1990. The diet of grey seals from the south-western North Sea
Ricker, W. E. 1954. Stock and Recruitment. Journal of the Fisheries Research Board of Canada,
from a century of tagging. Fish and Fisheries, 5: 185–214. doi: 10.1111/j.1467-
2679.2004.00141.x
prey consumption and switching by UK grey seals. ICES Journal of Marine Science 71: 81–89.
cod (Gadus morhua) on the eastern Scotian Shelf. Canadian journal Fisheries and Aquatic


Table 1. Fishery data sets used in the assessment model.

<table>
<thead>
<tr>
<th>Data type</th>
<th>Years</th>
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<tbody>
<tr>
<td>Landings by all fleets</td>
<td>1985-2005</td>
</tr>
<tr>
<td>Discards by all fleets</td>
<td>1985-2005</td>
</tr>
<tr>
<td>Combined landings and discards (total catch)</td>
<td>2006-2013</td>
</tr>
<tr>
<td>Scottish quarter 1 survey</td>
<td>1985-2010</td>
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<tr>
<td>Scottish quarter 4 survey</td>
<td>1996-2009</td>
</tr>
<tr>
<td>Irish quarter 1 survey</td>
<td>2003-2013</td>
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Table 2. Input quantities for the simulation model drawn from MCMC samples saved after fitting the stock assessment model.

<table>
<thead>
<tr>
<th>Quantity</th>
<th>Description</th>
<th>Usage</th>
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<tr>
<td>$f_{y,2013}$</td>
<td>Fishing effort multiplier in base year</td>
<td>Reference fishing effort</td>
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<tr>
<td>$\sigma^2_f$</td>
<td>Process error on fishing effort</td>
<td>Noise added to fishing effort</td>
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<tr>
<td>$N_{a,2013}$</td>
<td>Population number at age in base year</td>
<td>Base population for projections</td>
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<tr>
<td>$N_{1,y}$</td>
<td>Recruitment at age 1 in all years</td>
<td>Estimation of stock-recruitment parameters</td>
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<tr>
<td>$SSB_y$</td>
<td>Spawning stock biomass in all years</td>
<td>Estimation of stock-recruitment parameters</td>
</tr>
<tr>
<td>$PB_y$</td>
<td>Partial biomass available to seals in all years</td>
<td>Estimation of functional response</td>
</tr>
<tr>
<td>$s_{a,2013}$</td>
<td>Fishery selectivity at age in base year</td>
<td>Fixed fishery selectivity for projection</td>
</tr>
<tr>
<td>$q_{seal,y}$</td>
<td>Seal predation rate in all years</td>
<td>Estimation of functional response</td>
</tr>
<tr>
<td>$\alpha, \beta$</td>
<td>Parameters of the seal selectivity curve</td>
<td>Calculation of seal selectivity</td>
</tr>
<tr>
<td>$A,B$</td>
<td>Parameters of the Lorenzen equation</td>
<td>Estimation of natural mortality</td>
</tr>
</tbody>
</table>
Figure legends

Figure 1. Stock trends in (a) cod spawning stock biomass and (b) fishing mortality from three stock assessments. The solid line is the estimated trend from the most recent ICES assessment in 2014. The dotted line shows the ICES assessment conducted in 2002 and the filled points are the estimates from the current analysis which includes seal predation. Open circles in (a) show the partial biomass available to seals estimated from the model.

Figure 2. Relationships for SSB and recruitment, and seal predation rate and partial biomass. (a) The relationship between recruitment and spawning stock with a fitted Beverton-Holt model. (b) The relationship between seal predation rate and cod partial biomass with fitted functional response models. The grey dots are the MCMC samples. The black dots are the mean values of the MCMC samples and the solid line is the type II model fitted to the means to illustrate the form of the function used. The dashed line shows the loess model used in the sensitivity runs.

Figure 3. The total mortality (Z) for combinations of fishing mortality (F) and cod partial biomass (PB). The solid lines are contours of equal Z. Over-plotted are the values of Z from the historical estimates of fishing mortality and partial biomass from the stock assessment model joined as a time series with a dotted line. Earlier years are in the top right and recent years in the lower left.

Figure 4. The spawning stock biomass projected from 1985 using a type II functional response compared to the observed quantities from the stock assessment model. Lines show the percentiles ranging from 5 to 95% (dashed) from the projection model and points show the estimates from the stock assessment model.

Figure 5. The probability that the cod spawning stock biomass is lower than the baseline value in (a) year 5, and (b) year 50, for relative changes in fishing effort and seal population size. Contours show the probability levels. The dot in position (1,1) shows the 2013 state.
Figure 6. The median cod spawning stock biomass at equilibrium for relative changes in fishing effort and seal population size. The dot in position (1,1) shows the 2013 state and implies an SSB of around 40000 tonnes, higher than the 2013 estimate of about 11000 tonnes as estimated from the current analysis.

Figure 7. Comparison of short and long term projections made with a type II functional response (solid line), constant seal predation rate (dashed line), auto-correlated predation rate (dotted line) and “loess” functional response (dots and line) on the probability of stock decline and median SBB. Projections were performed assuming a constant seal population corresponding to the most recent population size.
Figure 1

(a) Spawning stock biomass (tonnes)

(b) Fishing mortality

Year

Spawning stock biomass (tonnes)

Fishing mortality

Year
Figure 2

(a) Recruitment ('000) vs. Spawning stock biomass (tonnes)

(b) Seal predation rate ($q_Y$) vs. Partial biomass (tonnes)
Figure 3

Fishing mortality

Cod partial biomass (tonnes)

0.8 1 1.2 1.6 1.8

0.2 0.4 0.6 0.8 1.0

0 10000 20000 30000 40000 50000 60000

Fishing mortality

Cod partial biomass (tonnes)
Figure 4

Spawning stock biomass (tonnes) vs. Year

50%
75%
95%
25%
5%

Year

0 5 10 15 20 25 30
0 20000 40000 60000 80000 100000 140000

Spawning stock biomass (tonnes)
Figure 5

(a) Relative fishing effort vs. relative seal population

(b) Relative fishing effort vs. relative seal population

(a) Relative fishing effort vs. relative seal population

(b) Relative fishing effort vs. relative seal population
Figure 7

The figure illustrates the relationship between the probability of decline and relative fishing effort for Year 5 and Year 50. The probability of decline increases with relative fishing effort. The SSB (standing stock biomass) decreases with an increase in relative fishing effort. The graphs show different scenarios represented by solid and dashed lines, indicating varying levels of fishing effort.